ALLUVIAL SCRUB VEGETATION OF THE SAN GABRIEL RIVER FLOODPLAIN, CALIFORNIA

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ABSTRACT

Composition, physiognomy, and development of floodplain vegetation are presented for three age zones of alluvial scrub on the San Gabriel River floodplain. The 19 species sampled are associated with the coastal sage scrub community, but the floodplain vegetation contains an unusually large proportion of arborescent, evergreen shrubs. Dominant species include *Rhus laurina, R. integrifolia, Lepidospartum squamatum, Eriogonum fasciculatum,* and *Opuntia* spp. The term "alluvial scrub" is suggested for this type of coastal sage scrub which is common on alluvial fans and floodplains along the San Gabriel and San Bernardino mountains. Mature stands are unusually diverse and appear to represent a climax vegetation that develops following severe, periodic flooding.

Gravelly alluvial fans and floodplains flanking the southern base of the San Gabriel and San Bernardino mountains support a distinctive assortment of shrubs and subshrubs characteristic of both coastal sage scrub and chaparral communities. This type of vegetation once covered much of the Los Angeles Basin (Ted L. Hanes, pers. comm., 1978) but is now confined to scattered remnants as a result of urbanization.

Although there are several references to this vegetation in the literature, no description of its composition or ecology is available. Hanes (1976) viewed it as a physiognomically unique expression of coastal sage scrub. Unlike typical coastal sage scrub composed of scattered drought-deciduous subshrubs and only occasional evergreens, this vegetation contains numerous evergreen chaparral shrubs in addition to a rich assemblage of subshrubs. In a description of structural and floristic variation within the coastal sage scrub, Kirkpatrick and Hutchinson (1977) mentioned an association occurring on fans and washes in cismontane southern California. They characterized this type by the tall stratum of evergreen shrubs and emphasized the "unrivalled structural complexity" of the association in comparison with the rest of the coastal sage scrub. In this study I surveyed the composition, physiognomy, and development of floodplain vegetation along the San Gabriel River.

STUDY SITE

Physiography and climate. The San Gabriel River floodplain has been isolated from urban impact since 1949 by a flood control dam

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and consequently retains an extensive stand of relatively undisturbed native vegetation. The San Gabriel River originates in the San Gabriel Mountains, Los Angeles County, and has a drainage area of 180,780 ha. After heavy rainstorms, the river carries debris eroded from unstable slopes, stream banks, and channels and deposits it where the river emerges from a narrow gorge onto the broad San Gabriel Valley. Thousands of years of flooding have created a gently sloping rocky plain underlain by alluvium up to 660 m thick.

The climate of the San Gabriel Valley and foothills is dry Mediterranean. The closest weather station to the study area is in San Gabriel, California, about 13 km from the flood basin. This station reports an average annual precipitation of 43 cm, most of which falls between November and April. Rainfall in the San Gabriel Mountains often falls in several extremely intense storms, which cause the destructive floods typical of the foothill regions. The two most recent floods on the San Gabriel River occurred in 1938 and 1969. Both of these were catastrophic, that in 1938 exceeding all previous floods on record by a considerable margin. These and older torrents have created a diverse alluvial topography consisting of a sparsely vegetated wash and higher, shrub-covered terraces.

Zonation. Aerial photographs of the flood basin reflect the presence of three physiographic zones of different ages, supporting distinct types of vegetation. The youngest zone, the wash, developed since the 1969 flood and supports scattered, short-statured, pioneer species. This wash contains remnants of a higher alluvial terrace destroyed by erosion during the 1939 flood. These older "islands" support large shrubs.

The terrace immediately above the wash supports dense scrub vegetation that developed since dam construction 30–37 years ago. The surface of this intermediate-level terrace represents an artificially altered substrate, as it was graded during construction.

The highest zone of the floodplain consists of an alluvial terrace that supports the diverse combination of shrubs and subshrubs that distinguish the fan and floodplain vegetation. The exact age of this stage of the floodplain community is not known, but shrub sizes and growth rings suggest 40 to 50 years.

Methods

Forty 30-m line intercepts were established randomly throughout the floodplain, and height class, frequency, and cover were recorded for each perennial species and for bare ground at 3-m intervals. Annual species were recorded but not sampled. Pairwise resemblance among the 40 intercepts was determined using the Bray-Curtis distance index for species composition. Intercepts were clustered using a flexible sorting strategy based on a sorting coefficient of -0.25 to

TABLE 1. RELATIVE COVER OF ALLUVIAL SCRUB SPECIES FOR EACH SITE SAMPLED. Site numbers correspond to those given in Fig. 1. Values are based on total plant cover, bare ground excluded.

	Sites																			
	Pioneer Zone										Intermediate Zone									
Species	1	2	3	8	9	10	24	34	35	36	4	5	6	21	37	38	39	40	41	42
Lepidospartum squamatum	27	25	27	100	68	21	10	21	23	89	—	—	21	14	13	19	—	10	—	13
Eriogonum fasciculatum	—	73	—	—	—	46	39	26	36	—	100	66	79	86	87	80	94	90	96	89
Chrysopsis villosa	—	—	30	—	27	32	33	10	11	—	—	—	—	—	—	—	—	—	—	—
Baccharis glutinosa	57	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Penstemon spectabilis	—	—	37	—	—	—	—	18	17	11	—	—	—	—	—	—	—	—	—	—
Lotus scoparius	—	—	—	—	—	—	18	24	12	—	—	—	—	—	—	—	6	—	2	—
Yucca whipplei	—	14	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhus laurina	—	—	—	—	—	—	—	—	—	—	—	31	—	—	—	—	—	—	—	—
Rhus integrifolia	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Salvia mellifera	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Ribes aureum	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Gutierrezia bracteata	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Opuntia occidentalis	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Opuntia parryi	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Haplopappus pinifolius	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Marah macrocarpus	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Rhamnus crocea	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Eriodictyon trichocalyx	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Artemisia californica	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

TABLE 1. Continued.

Species	Mature Zone																			
	7	11	12	13	14	15	16	17	18	19	20	25	26	27	28	29	30	31	32	33
Lepidospartum squamatum	4	—	—	—	3	—	—	1	—	5	12	10	4	29	3	20	2	14	5	—
Eriogonum fasciculatum	70	2	21	—	11	2	40	—	4	7	12	17	54	7	—	—	8	17	5	23
Chrysopsis villosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Baccharis glutinosa	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Penstemon spectabilis	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
Lotus scoparius	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Yucca whipplei	—	—	—	—	—	—	—	—	4	6	—	—	—	24	—	—	3	4	6	50
Rhus laurina	—	26	5	27	50	—	40	—	48	40	—	—	—	24	87	18	63	21	—	—
Rhus integrifolia	25	—	—	16	2	95	—	—	—	—	30	23	—	—	—	52	—	30	39	—
Salvia mellifera	63	5	19	3	—	—	11	71	35	21	—	—	—	—	—	—	—	—	—	—
Ribes aureum	—	41	55	24	—	—	3	6	—	21	7	—	—	5	—	1	18	12	13	—
Gutierrezia bracteata	—	—	—	8	—	—	—	—	—	—	—	20	33	—	—	—	—	—	—	—
Opuntia occidentalis	—	11	—	17	21	2	6	3	—	2	21	1	3	—	4	6	3	5	19	27
Opuntia parryi	—	12	—	—	—	—	—	15	—	—	—	—	—	—	—	—	—	—	1	—
Haplopappus pinifolius	—	—	—	—	—	—	—	3	—	—	12	—	—	—	—	—	—	—	—	—
Marah macrocarpus	—	—	—	5	—	—	—	—	9	—	11	—	2	—	—	—	—	—	—	—
Rhamnus crocea	—	2	—	—	—	—	—	—	—	—	—	24	—	—	—	—	—	—	12	—
Eriodictyon trichocalyx	—	—	—	—	14	—	—	—	—	—	—	—	—	11	2	1	—	—	—	—
Artemisia californica	—	—	—	—	—	—	—	—	—	—	—	—	3	—	2	—	—	—	—	—

make group entry more difficult as the group enlarged. This method facilitates formation of numerous, distinct clusters (Smith, 1977).

To approximate the maximum age of each vegetation type, increment cores were taken from *Rhus laurina* (nomenclature follows Munz, 1974), the largest species occurring in all three zones. All perennial plants sampled were classified by lifeform (Mueller-Dombois and Ellenberg, 1974).

Quantitative measures of species diversity and lifeform diversity were made for each zone according to the Shannon-Wiener diversity function (Pielou, 1974).

To characterize the substrates of the three different zones, contents of three pits (0.3 m on each side and 0.3 m deep) from each zone were sorted into five size classes ranging from fine sand to rocks greater than 20 cm in diameter, and the relative volume of each class determined by water displacement. Soil texture and organic content were determined from a minimum of four samples in each zone, the former by standard hydrometer technique, and the latter by ash-free combustion at 500°C for 12 hours. Differences in species diversity, lifeform diversity, and soil among the three vegetation types were tested by ANOVA at $\alpha = 0.05$.

Results

Composition

Sample plots on the alluvial plain supported 19 perennial species, although others were observed outside the 40 plots (Table 1). All species observed except *Juniperus californica* were common, native elements of either chaparral or coastal sage scrub communities.

Cluster analysis based on plant cover generated three major groups of sites that corresponded to vegetation zones observed in the field with only two discrepancies, sites 25 and 26 (Fig. 1). The dendrogram indicates relative uniformity of vegetation in the pioneer and intermediate zones. In contrast, dissimilarity of sites in the mature zone is high.

Pioneer zone. This zone consisted of young perennials, forming an average total plant cover of only 10 percent (Fig. 2). The zone supported seven of the 19 perennials sampled (Table 1), and had an intermediate species diversity ($H' = 0.37$).

Intermediate zone. Vegetation of the intermediate zone was uniform and relatively dense, with an average plant cover of 51 percent, dominated by *Eriogonum fasciculatum* (Fig. 2). Dead material made up a conspicuous fraction of this vegetation. Scattered tall shrubs overtopped the scrub layer (Fig. 3), but were infrequent and, with the exception of *Rhus laurina,* did not occur on sample plots. Only four

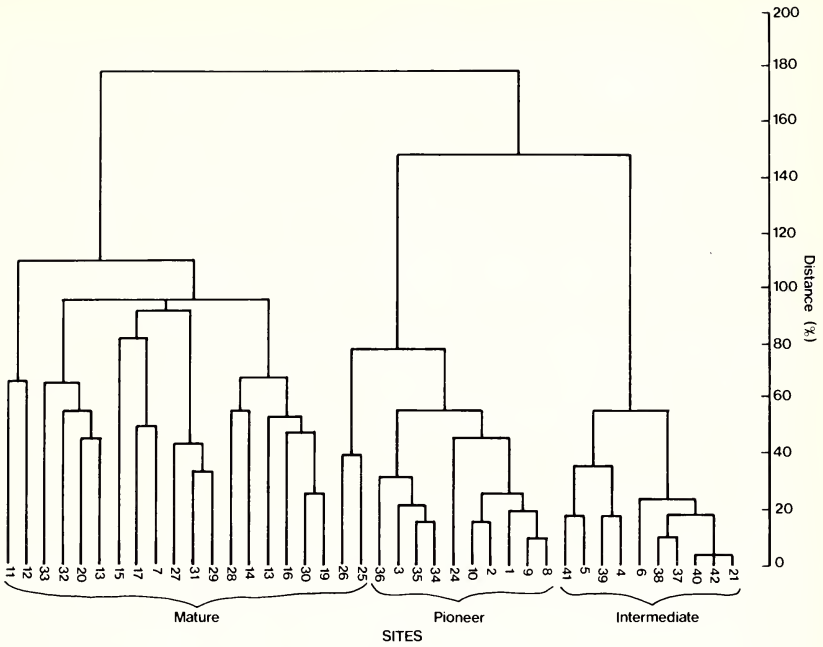

FIG. 1. Dendrogram generated from Bray-Curtis cluster analysis.

of the 19 dominant perennials were sampled in this zone (Table 1), attesting to its low diversity ($H' = 0.15$).

Mature zone. The mature terrace flanking the wash and the uneroded alluvial "islands" left intact within the wash supported the greatest number of species (16) and the highest plant cover (Fig. 3, Table 1). This assemblage was not only rich in species, but had the most complex vertical structure with three distinct strata (Fig. 3).

Patterns in species composition on the mature terrace were associated with topography. The terrace consisted of two levels: higher, undissected portions and shallow drainages that once served as flood channels. Higher portions were dominated by large evergreen shrubs, predominantly *Rhus laurina* and *R. integrifolia. Ribes aureum, Rhamnus crocea, Sambucus mexicana,* and *Juniperus californica* also contributed to this stratum. *Ribes aureum* was the only tall shrub represented by seedlings and saplings as well as mature individuals. Subshrubs and cacti formed a variable stratum between larger, scattered shrubs (Fig. 3). This stratum was especially well developed in shallow drainages dissecting the terrace where larger shrubs were absent.

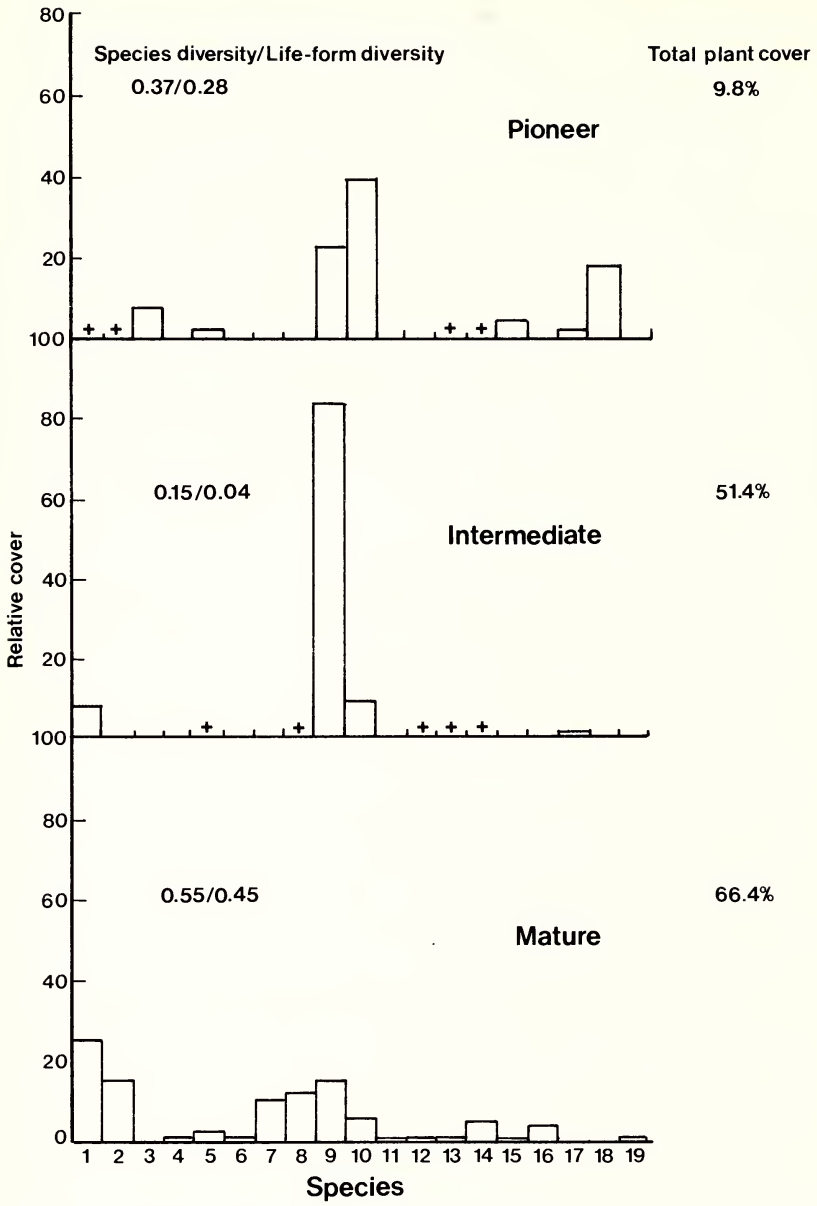

FIG. 2. Average relative cover of floodplain species and diversity of each zone. "+" indicates species observed but not sampled. Values are based on total plant cover, bare ground excluded. Key to plant species: 1) *Rhus laurina*; 2) *Rhus integrifolia*; 3) *Baccharis glutinosa*; 4) *Rhamnus crocea*; 5) *Yucca whipplei*; 6) *Eriodictyon trichocalyx*; 7) *Ribes aureum*; 8) *Salvia mellifera*; 9) *Eriogonum fasciculatum*; 10) *Lepidospartum squamatum*; 11) *Artemisia californica*; 12) *Haplopappus pinifolius*; 13) *Opuntia parryi*; 14) *Opuntia occidentalis*; 15) *Penstemon spectabilis*; 16) *Gutierrezia bracteata*; 17) *Lotus scoparius*; 18) *Chrysopsis villosa*; 19) *Marah macrocarpus*.

Seven of the 16 species encountered on the mature sites had an average relative cover greater than 5 percent of the total plant cover (Fig. 2). This distribution of dominants resulted in the heterogeneous appearance of the mature floodplain vegetation, which was reflected in relatively high diversity ($H' = 0.55$).

In portions of the mature community, the arborescent and subshrub strata formed impenetrable thickets but nearly 34 percent of the terrace consisted of open patches supporting only annual plants, particularly *Camissonia bistorta, Cryptantha muricata, Phacelia distans,* and *Schismus barbatus*. This zone was the only one with a dense herbaceous layer.

Trends in lifeform composition of the three zones paralleled those of species composition (Fig. 2). The greatest number and most even distribution of lifeforms occurred on the mature terrace.

Ages

Stand ages based on analysis of *Rhus laurina* increment cores indicated the largest individuals in the intermediate zone developed since approximately 1951 with a maximum age of 25–30 years. Individuals in the pioneer zone were 7–14 years old, indicating that some survived the record floods of 1969. Ring counts showed the largest individuals in the mature zone were 35–47 years old. Because *Rhus laurina* is a resprouting species, underground parts are potentially much older. The presence of dead snags and rotten root crowns toward the center of the multi-stemmed trees was evidence that some crowns were resprouts from much older, underground lignotubers.

Eriogonum fasciculatum and *Lepidospartum squamatum* were common both as colonizers of the pioneer zone and as species of the mature shrubland. In the latter zone, however, these species were reduced mostly to isolated, senescing individuals.

Substrate

Substrate in all three age zones consisted of flood deposits. There was no significant difference between the mean volume of small size classes in the three age zones, but distribution of boulders varied significantly among zones. The pioneer zone was unique for its boulder and debris-strewn nature (25 percent cover), a result of torrential 1969 storm runoff. Substrate of the intermediate-aged zone was indicative of its artificially disturbed character. Boulders were conspicuously absent. Ground surface of the mature zone was quite heterogeneous. Large expanses consisted only of small pebbles and deep soil, but such areas were interrupted by rocky drainages containing scattered boulders and large rocks.

Floodplain soils were high in sand (86–98 percent) and low in organic matter (0.25–0.38 percent). Wash soil was nearly pure sand (98–99 percent), whereas soils in the intermediate-aged zone had measur-

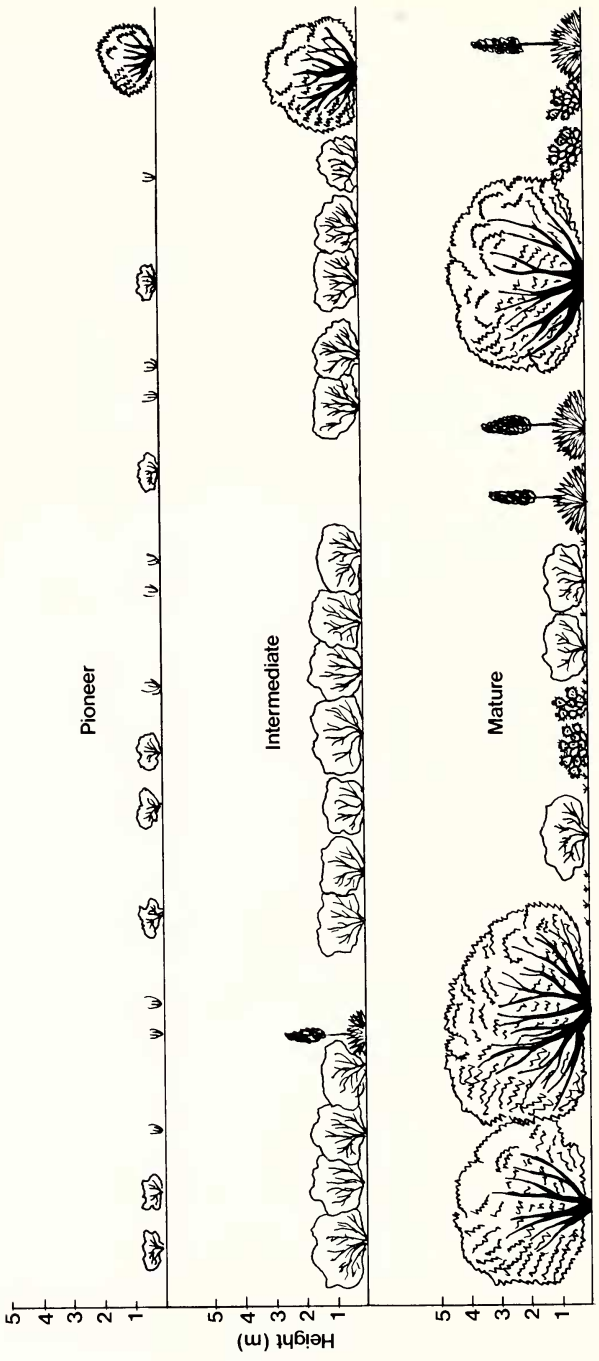

FIG. 3. Diagrammatic profile of floodplain vegetation.

able amounts of silt and clay. Soils of the mature zone were deeper and finer than those of the younger zones and contained 13 percent silt. Soil organic content increased with age of substrate.

Discussion

The floodplain vegetation has strong floristic affinities with the coastal sage scrub type, as documented by Kirkpatrick and Hutchinson (1977), and should be considered a part of it. Coastal sage scrub is typically dominated by subligneous, drought-deciduous plants, but dominance of evergreen, woody shrubs in the tallest synusia gives the floodplain association a quality unlike typical coastal sage scrub. I propose the term "alluvial scrub" for the association, a name that depicts both its physiographic position and its physiognomy as a shrubland dominated by woody shrubs and small trees (Mueller-Dombois and Ellenberg, 1974).

Mooney (1977) found a trend toward increasing evergreenness with decreasing aridity in coastal sage scrub. He related this to physiological differences between evergreen shrubs and drought-deciduous shrubs, the former being favored in habitats of short drought duration because of their long period of low gas exchange. *Platanus racemosa,* a winter-deciduous, riparian tree, occurs occasionally on the floodplain, also indicating that the physical conditions of the floodplain are more mesic than those prevailing in other, more typical, coastal scrub stands where *Platanus* is absent. Both the high percentage of evergreens and the occurrence of *Platanus* place the alluvial scrub association toward the mesic end of the aridity gradient in coastal sage scrub.

Unique floodplain species. Alluvial scrub of the San Gabriel River floodplain is distinctive because it is structurally and floristically diverse. In addition, the area supports species that should be recognized as unusual because of their distribution. *Lepidospartum squamatum* is the one species occurring on the floodplain that is faithful to alluvial substrates. Perhaps *Lepidospartum* requires mechanical scarification and therefore is confined to drainages. This species is considered indicative of the alluvial scrub association. Occurrence of *Juniperus californica* on the floodplain is unusual because it is typically a species occupying desert slopes (Munz, 1974). Perhaps major drainages, such as the San Gabriel River, act as corridors for dispersal of juniper seeds from dry, interior mountain slopes. Dominance of *Rhus integrifolia,* primarily a coastal species, is also noteworthy this far inland.

Coocurrence of species and lifeforms of both desert and coastal affinities contributes to the diversity of the alluvial scrub association. It appears that the floodplain, with its sandy substrate yet mild Mediterranean climate, provides the unusual combination of physical factors that facilitates coocurrence of these types.

Succession. Cooper (1922) assumed pioneer vegetation of washes was successionally related to the climax community of older terraces. If this assumption is valid, the youngest zone of the San Gabriel River floodplain, if not flooded for a long period of time, should eventually support vegetation like that of the oldest terrace. Results of this analysis support such an inference. Many species dominant in the older zone also occur in the youngest one, indicating the two habitats are sufficiently comparable to support the same general vegetation, given adequate time for species enrichment. This can be substantiated only by long-term observation of the area.

Inferring that different vegetation types represent a chronological sequence of community development is justifiable only if all other ecological factors, especially climate and substrate, are nearly constant. Substrates of the wash and mature terrace are equivalent in origin, both formed by similar processes of erosion and deposition. The different soil textures found, however, are not necessarily related to different ages of the two zones. Debris basins and flood control channels built since 1939 have altered patterns of sediment deposition and probably are responsible for the textural differences. Old terraces are no longer being flushed of their finer material since floods have been confined to narrow channels. Relatively slight differences in soil texture are probably not sufficient to promote different types of vegetation, however. The coarser soil of the wash will probably eventually support a dry expression of the mature community, as soil moisture stress is gradually alleviated through time by wind deposition of fine-grained particles, shading by established shrubs, and incorporation of organic material into the soil.

Succession after flooding begins with the invasion of the pioneer shrubs *Eriogonum fasciculatum* and *Lepidospartum squamatum* and numerous herbaceous perennials including *Lotus scoparius* and *Chrysopsis villosa.* Occasional individuals of *Baccharis glutinosa,* typical of mesic, riparian habitats, contribute to plant cover. Cover and height increase as the community is enriched by colonizing species, including *Yucca whipplei, Opuntia occidentalis, Haplopappus pinifolius, Eriodictyon trichocalyx,* and *Salvia mellifera.* If flooding is not violent enough to excavate deep root systems of mature shrubs such as *Rhus laurina* and *Rhamnus crocea,* they may resprout and assume dominance early in succession. Eventually, the vegetation is dominated by scattered, tall, resprouting shrubs surrounded by low-growing subligneous shrubs, cacti, and *Yucca.*

The absence of seedlings of climax shrub species, even after the record rainfall of 1978, suggests that establishment by seed of these species is a rare event in the alluvial habitat. Conditions promoting establishment of existing *Rhus laurina* individuals are not known, nor is the explanation for uniformity of ages of the largest specimens. Apparently, individuals resprouted since some event approximately

40–50 years ago. A major flood (1939?) with force to destroy aboveground plant material is the most likely explanation. In contrast to the dominant evergreens, reproduction by seed of shrubs of the lower stratum occurs frequently.

Regeneration of evergreen shrubs may be stimulated by floods of sufficient power to inundate the higher terraces, as flood waters may saturate the normally well-drained soils and import inorganic nutrients and sources of organic matter. If such is the case, composition of mature vegetation may gradually shift toward a more typical coastal sage scrub with a smaller proportion of evergreen species, because flood control measures have isolated the upper terraces from most floods. However, it is likely that a major flood need inundate the upper terrace on the order of only once or twice per century to stimulate establishment and growth of evergreen seedlings and the upper terrace is still within the range of such infrequent flood waters. Several consecutive years of above-average rainfall and mild temperatures may also provide the conditions necessary to insure perpetuation of climax species. Germination studies of *Rhus laurina* and similar species could elucidate the ecological requirements for regeneration.

Low diversity of both species and lifeforms in the intermediate zone indicates the effect of unnatural disturbance on alluvial scrub vegetation. Bulldozing approximately 30 years ago apparently favored establishment of *Eriogonum fasciculatum* at the expense of other colonizing species and has led to the development of a structurally and floristically simple vegetation. The occurrence of emergent shrubs suggests the zone will eventually succeed to a more complex assemblage.

Differences in species and lifeform diversity among the three stages of alluvial scrub support general features of succession suggested by Drury and Nisbet (1973). Community development on the floodplain seems to combine two processes that result in increased species and lifeform diversity: 1) emergence into prominence of species and lifeforms present at the start, and 2) enrichment by continual colonization of the site.

Alluvial scrub is a pulse-stable climax vegetation (Odum, 1971) adapted to occasional, destructive flooding. Species either recolonize flooded areas by seed or resprout from underground tissues. Alluvial scrub is physiognomically distinct from chaparral and typical coastal sage scrub communities and should be recognized as a diverse expression of the latter, rich in both species and lifeforms.

Because urban and industrial developments are destroying this unique type of coastal sage scrub, support should be given to preservation of existing stands.

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NOTEWORTHY COLLECTIONS

Cucurbita foetidissima H.B.K. (Cucurbitaceae).—USA, WY, Laramie Co., w. edge of Granite, 2225 m, 5 Aug 1979, *Dorn 3344,* RM. Along a railroad embankment where observed for 3 years.

Previous knowledge. CO and NE, s. to TX, CA, and Mex. (Herbarium consulted: RM; published sources: Bailey, Gentes Herb. 6:267–322, 1943; Barkley, Atlas fl. Gt. Plains, 1977; Harrington, Man. pls. Colorado, 1954). *Diagnostic characters.* Keys to *Echinocystis lobata* in Dorn (Man. vasc. pls. Wyoming, 1977, p. 581) but is a perennial herb; lvs truncate to cordate at base, 10–30 cm long, scabrous; corolla 6–15 cm long; calyx campanulate, 5-lobed; fr globose to ovoid-globose, striped or mottled green, 5–10 cm long.

Significance. First report for WY. About 96 km from nearest known population in Banner Co., NE.

Elymus innovatus Beal (Gramineae).—USA, WY, Crook Co., Cold Springs Creek (T48N R60W S9 NE¼), 1875 m, 16 Sep 1979, *Lichvar 2491,* RM. Frequent in partially open meadow near n.-facing slope. Associates included *Calamagrostis inexpansa, Picea glauca,* and *Pyrola elliptica.*

Previous knowledge. AK to B. C., e. to Alta. and s. to MT, SD, and WY. (Herbaria consulted: NY, RM, SDU, UC; published sources: Bowden, Canad. J. Bot. 37:1148, 1959; Hitchcock, A. S., Man. grasses U. S., 1950; Hitchcock, C. L., et al., Man. vasc. pls. Pac. Northw. II., 1964). *Diagnostic characters.* Culms tufted, to 1 m high from rhizomes; lvs mostly 1–5 mm wide; glumes 4–10 mm long, villous, somewhat bristle-like; lemmas mostly 7–9 mm long, mostly villous, awn 1–10 mm long.